

Hindwings are unnecessary for flight but essential for execution of normal evasive flight in Lepidoptera

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In Lepidoptera, forewings and hindwings are mechanically coupled and flap in synchrony. Flight is anteromotoric, being driven primarily by action of the forewings. Here we report that lepidopterans can still fly when their hindwings are cut off, a procedure reducing their total wing surface, on average, by nearly one half. However, as we demonstrate by analysis of three-dimensional flight trajectories of a moth and a butterfly (*Lymantria dispar* and *Pieris rapae*), hindwing removal causes lepidopterans to incur a loss in both linear and turning acceleration, so that they are unable to exercise their normal flight maneuverability. Without hindwings they still are able to zigzag aerially (the ablation has no effect on their turning radius in flight) but at lesser speed and therefore less evasively. Consequently, hindwings in the expanded state in which they occur in lepidopterans seem to contribute in an essential way to lepidopteran survival. Moths in today's world, we argue, may rely on their evasive flight primarily to avoid capture by bats, whereas butterflies, which we propose advertise their evasiveness collectively through shared aposematism, may depend upon it primarily for defense against birds. Aerial agility thus may be the chief adaptive asset derived by lepidopterans from possession of oversized hindwings.

aposematism | coloration | defense | flight maneuverability | mimicry

Butterflies, in nature, are highly visible. Conspicuously colored and endowed with a large wing-to-body ratio, they can be spotted and recognized from further away than any other insects. Children can tell butterflies from other insects even when they are too young to distinguish other insects from one another.

There is something else that children are quick to learn, particularly if they take up butterfly collecting as a hobby. Butterflies are hard to catch. They are erratic fliers that cannot be caught simply by anticipating their flight trajectory and reaching for them. It takes a net to sweep them up, a net of considerable size, lest the effort prove futile.

What a youngster can learn, a bird might know as well. A bird, we suggest, could learn or inherently know that brightly colored airborne prey, discernable from afar, is not worth the chase. Too elusive to catch and, because of their scales, too slippery to hold, butterflies are prone to disappoint even if actually caught, given that they are “mostly wrapper and little candy.” Birds simply might write butterflies off, and, as a result of learning or genetic predisposition, relegate them all to the category of the undesirable, treating them as they treat noxious insects that they disregard.

The argument need not apply equally to all birds, for indeed there are some that prey on butterflies (1–7), but it could be pertinent to many or most. Butterflies, we propose, are a mimetic assemblage in which showiness, in the sense of spectral contrast, is the shared aposematic trait. Implicit in our argument is that evasiveness, defined as “the ability to fly quickly, at varying speed and direction,” evolved early within the lepidopteran stock, providing the aversive trait that eventually was advertised by the butterflies' display of color. An unexpected observation provided a clue to what enables lepidopterans to fly

erratically. We discovered that when their hindwings are severed with scissors, butterflies and moths can still fly, although not as rapidly nor as evasively as they normally do. The hindwings, which are coupled mechanically to the forewings and flap in synchrony with the forewings (flight in lepidopterans is anteromotoric, being driven primarily by the forewings) (6), although dispensable for flight, seemed essential for the execution of full-speed aerial maneuvering. They are part of the lepidopteran armamentarium. Here we present observational and quantitative data in support of this notion.

The observational data were obtained simply by noting visually how hindwing removal affected flight performance of butterflies and moths released by hand outdoors. For each species a determination also was made of the ratio of hindwing area to total wing area.

The quantitative data were derived from 3D video recordings of flight trajectories, obtained with two lepidopterans, the cabbage butterfly (*Pieris rapae*) and the gypsy moth (*Lymantria dispar*) (Fig. 1), chosen because of ready availability and diurnal habits (in the gypsy moth only the male flies, and it does so in the daytime). With both species, we determined, separately for intact and hindwing-deprived individuals (the latter henceforth referred to as “de-winged”) (i) the trajectories they undertook in free flight and (ii) their wingbeat frequencies. From these data we computed two sets of values: kinematic and geometric. With respect to kinematic parameters, we computed (for a given flight) mean speed (v), mean magnitude of the linear acceleration (a), and mean magnitude of the normal, or turning, acceleration (a_N), signifying, respectively, the rate of advance along the flight path, the rate of change of velocity, and the rate of change of direction. As regards geometry, we computed the mean radius of curvature (r), a measure of the turning radius along the flight path.

Results

Observational Data. Without exception, all butterflies and moths tested proved capable of sustained flight after severance of the hindwings (Table 1). Neither the length of time they remained airborne nor their ability to maintain altitude seemed to be affected by the operation. Distances traversed before the individuals alighted or vanished from view were routinely in excess of 20 m. Some of the moths that could not be retrieved after their release were identified to family only. One overall conclusion that we derived from these observations was that without their hindwings all these lepidopterans seemed to fly more slowly.

Hindwing Area. Hindwings (Table 1) made up almost half of the total wing area for butterflies ($49 \pm 3\%$ [SD]; $n = 19$ species) and moths ($44 \pm 6\%$ [SD]; $n = 25$ species). The mean value for

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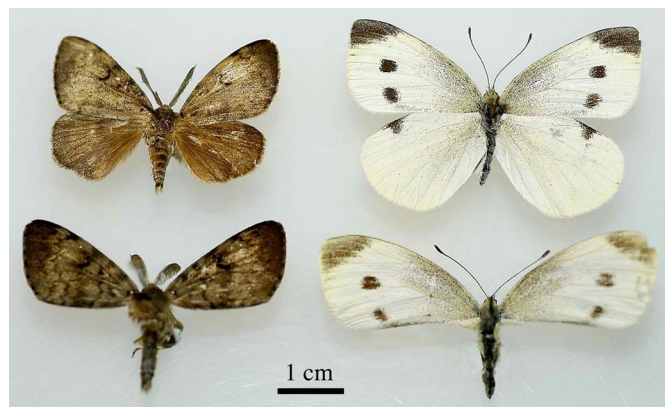


Fig. 1. Gypsy moth (*Lymantria dispar*) (Left) and cabbage butterfly (*Pieris rapae*) (Right), both normal (Upper) and de-winged (Lower).

moths is lower because in some moths (e.g., the Sphingidae) the hindwing area is only about a third of the total wing expanse.

Quantitative Data. As is clear from Table 2, hindwing removal in *P. rapae* and *L. dispar* had a significant effect on most measures of flight performance (the exceptions are indicated by bold type). First, as was already evident from the observational tests, hindwing ablation caused both *P. rapae* and *L. dispar* to fly slower (despite, in the case of *L. dispar*, an increase in wingbeat frequency). In both lepidopterans, linear and turning accelerations were reduced sharply after hindwing severance, indicating that, at least in part, their broad-surfaced hindwings enable these insects to exercise their normal aerial maneuverings. (Note that turning acceleration decreased whether it was computed in three dimensions or strictly in the horizontal plane.) Also noteworthy is that hindwing removal had no effect on the radius of curvature of the trajectories. De-winged individuals, in other words, were not forced by loss of hindwings to alter their flight path. They remained capable of zigzagging aerially like the controls but were prone to perform such maneuvers at a slower pace.

Examples of flight trajectories are depicted in 3D in Fig. 2 A–D. One trajectory also is shown with the error of measurement factored in (Fig. 2E) and again with the orthogonal projections plotted separately (Fig. 2F).

Discussion

Our preliminary data, with hand-released individuals, left no doubt that in butterflies and moths hindwing removal generally does not abolish the ability to fly. This finding perhaps was to be expected, given the anteromotoric nature of lepidopteran flight (6). Anteromotorism also would have predicted that lepidopterans should be unable to withstand the loss of forewings. Indeed, tests that we undertook with a number of butterflies (*Pieris rapae*, *Eurema lisa*, *Phoebes sennae*, and *Colias eurytheme*) and moths (*L. dispar*, *Utetheisa ornatrix*) showed that these species are rendered altogether flightless when deprived of their forewings. Still, it certainly was surprising that lepidopterans were able to fly as well as they did after what essentially was total ablation of their hindwings. Why do the lepidopterans have such a large wing expanse, one might ask, when nearly half that surface is dispensable? Clearly, as evidenced by our quantitative data, dispensability cannot be equated with redundancy in the assignment of function to wing surface area in Lepidoptera. The lepidopteran hindwings, in their full expanse, far from being superfluous, seem to be essential for the execution of normal erratic flight. It is through hindwing possession, and doubtless partly in consequence of the hindwing's large size, that lepidopterans are able to attain high levels of flight speed and directional

Table 1. Moths and butterflies that proved capable of flying with the hindwings removed

Family	Genus/Species
Moths	
Geometridae	<i>Scopula limboundata</i> (50) <i>Ennomos subsignaria</i> (48) <i>Biston betularia</i> (40) <i>Lyctosis unitaria</i> (44) Five unidentified species
Lasiocampidae	<i>Malacosoma americanum</i> (44)
Saturniidae	<i>Arctias luna</i> (52) <i>Automeris io</i> (45) <i>Antheraea polyphemus</i> (45)
Sphingidae	<i>Smerinthus jamaicensis</i> (34) <i>Pachysphinx modesta</i> (33) <i>Manduca sexta</i> (35)* Two unidentified species
Notodontidae	<i>Pheosia rimosa</i> (43) Two unidentified species
Arctiidae	<i>Lophocampa caryae</i> (42) <i>Pyrrharctia isabella</i> (43) <i>Grammia parthenice</i> (48) <i>Apantesis phalerata</i> (53) <i>Haploa confusa</i> (49) <i>Ctenucha virginica</i> (36) <i>Utetheisa ornatrix</i> (50)*
Lymantriidae	<i>Lymantria dispar</i> (50)
Noctuidae	<i>Harrisimemna trisignata</i> (39) <i>Acronicta</i> sp. (47) <i>Catocala neogama</i> (43) <i>Catocala</i> sp. (47) <i>Noctua pronuba</i> (49) Three unidentified species
Butterflies	
Papilionidae	<i>Papilio polyxenes</i> (52) [†] <i>Papilio cresphontes</i> (50)
Pieridae	<i>Colias eurytheme</i> (50) <i>Colias philodice</i> (53) <i>Colias cesonia</i> (52) <i>Phoebis sennae</i> (49) <i>Eurema lisa</i> (50) <i>Pieris rapae</i> (48)
Nymphalidae	<i>Phyciodes tharos</i> (44) <i>Agraulis vanillae</i> (49) <i>Heliconius charitonius</i> (43) <i>Speyeria cybele</i> (46) <i>Vanessa cardui</i> (48) [†] <i>Limenitis archippus</i> (49) [†] <i>Danaus plexippus</i> (52) <i>Danaus gilippus</i> (50) [†] <i>Junonia coenia</i> (51)
Satyridae	<i>Cercyonis pegala</i> (53)
Hesperiidae	<i>Epargyreus clarus</i> (50)

Numbers give the ratio (%) of hindwing area to total wing area. All individuals were field collected, except those that were obtained as pupae from a commercial source (*), and those that were laboratory-raised (†).

inconstancy (that is, maneuverability), the two parameters that in combination so often determine the elusiveness of prey. To avoid capture it is not obligatory for a given prey species to be able to outpace the predator. It may suffice for it to be able to zigzag faster than its pursuer, something that it might well be able to do if empowered by high turning acceleration (8). Lepidoptera, it seems, have achieved some of their adaptive success through evolutionary exploitation of this paradigm.

Table 2. Summary of flight data

	<i>P. rapae</i>		<i>L. dispar</i>	
	Intact	De-winged	Intact	De-winged
Speed in m/s	2.37 ± 0.436 (N = 41)	1.77 ± 0.363 (N = 41)	1.57 ± 0.418 (N = 16)	1.22 ± 0.331 (N = 11)
Acceleration in m/s ²	8.48 ± 2.08 (N = 41)	6.19 ± 1.34 (N = 41)	8.94 ± 2.42 (N = 16)	5.09 ± 1.13 (N = 11)
Normal acceleration in m/s ²	7.64 ± 2.08 (N = 41)	5.39 ± 1.32 (N = 41)	8.46 ± 2.49 (N = 16)	4.62 ± 1.22 (N = 11)
Normal acceleration in the horizontal plane in m/s ²	5.18 ± 1.86 (N = 41)	3.54 ± 1.23 (N = 41)	5.34 ± 2.17 (N = 16)	3.10 ± 1.05 (N = 11)
Radius of curvature in m	1.17 ± 1.58 (N = 41)	0.986 ± 1.51 (N = 41)	0.428 ± 1.76 (N = 16)	0.481 ± 1.47 (N = 11)
Wingbeat frequency in Hz	11.8 ± 2.13 (N = 10)	13.2 ± 1.16 (N = 10)	26.8 ± 2.23 (N = 11)	29.6 ± 1.57 (N = 10)

Entries give mean ± SD, with sample size in parentheses. Differences between intact and de-winged condition, in the two species, are significant ($P < 0.05$) for all parameters, except for the three comparisons highlighted by bold type. Values pertaining to radius of curvature assume log-normal data.

Much has been written about butterfly flight and its morphological and physiological determinants (6, 9–15). The evasive nature of butterfly flight is recognized (10–13, 16, 17), as is the

possibility that showiness has deterrent value in these insects (11, 12, 17, 18). Nowhere, however, has evidence been presented linking flight performance with evolutionary hindwing enlarge-

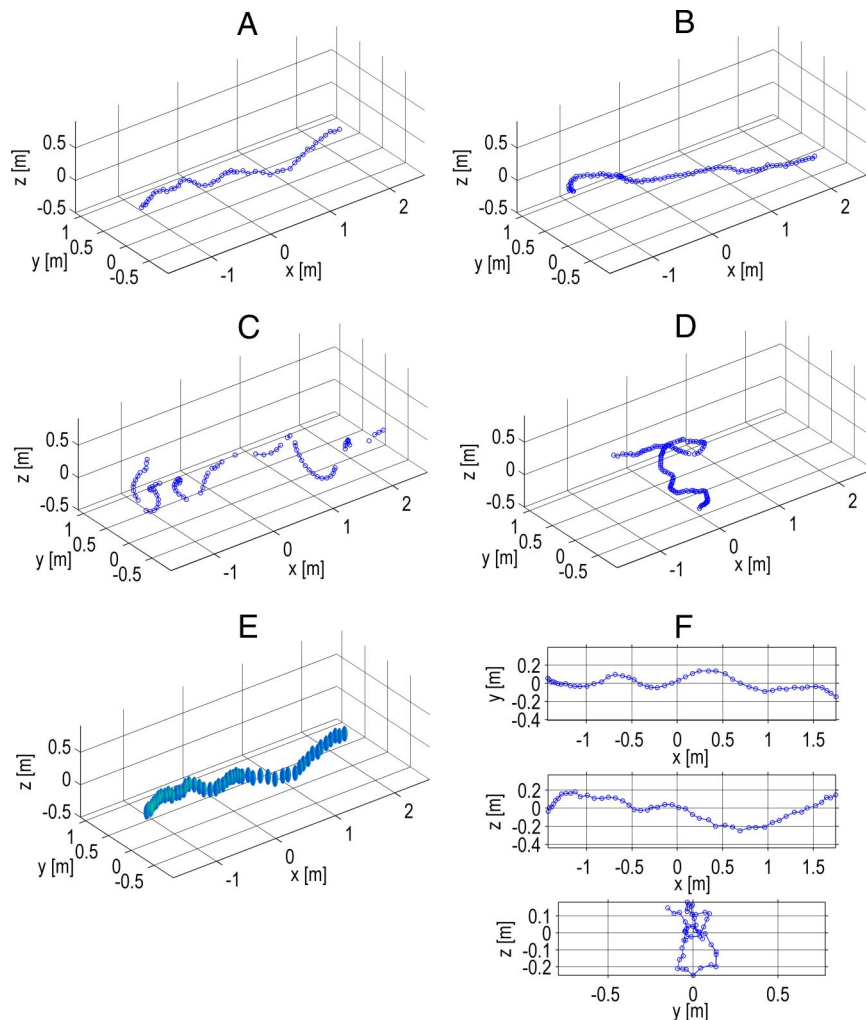


Fig. 2. Sample trajectories. Plotted are flights of (A) an intact *P. rapae* (duration 1.60 s) with mean values of speed ($v = 2.26$ m/s), acceleration ($a = 9.88$ m/s²), turning acceleration ($a_N = 9.36$ m/s²), and radius of curvature ($r = 0.936$ m); (B) the same *P. rapae*, de-winged (duration 2.87 s) with $v = 1.47$ m/s, $a = 4.22$ m/s², $a_N = 4.04$ m/s², and $r = 1.24$ m; (C) an intact *L. dispar* (duration 4.07 s) with $v = 1.77$ m/s, $a = 13.4$ m/s², $a_N = 13.3$ m/s², and $r = 0.275$ m; (D) a de-winged *L. dispar* (duration 4.30 s) with $v = 0.839$ m/s, $a = 4.25$ m/s², $a_N = 3.73$ m/s², and $r = 0.318$ m. (E) The same plot as in (A), but with the data points depicted as ellipsoid volumes in which errors are expressed as the lengths of the major and semi-major axes. In (F), the trajectory in (A) is shown projected separately onto the three orthogonal planes.

ment in lepidopterans, nor have any of the details of this linkage been elucidated by analysis of 3D recordings of flight trajectories. Of interest are earlier studies establishing a correlation, in both butterflies and diurnal moths, between thoracic flight muscle mass and palatability (11). Palatable species, in probable consequence of being more avidly pursued, were found to have proportionally more flight muscle than unpalatable species and to be faster fliers. Unpalatable species, less pressed to invest in flight muscle production, gained body space that they could allocate to gut and gonads. These findings, although underscoring the possibility that lepidopteran flight may have been subject to later evolutionary refinement, should not detract from what we propose is the fundamental reality, namely that, early on, lepidopterans as a group were enabled by hindwing expansion to acquire the evasive characteristics that are defining of their flight and perhaps are responsible, in large measure, for their adaptive success.

When, in the course of their evolution, did evasive flight arise as an adaptive trait in Lepidoptera? Evasive flight, defined as the ability to zigzag aerially at high speed, certainly was not “invented” by butterflies, because moths also seem to make use of the behavior. Moths, in fact, may have been first to put evasive flight to use, exploiting it for defense against nocturnal hunters, eventually including bats, the principal winged enemies plaguing night-flying moths. Butterflies, as the descendants of moths, thus may have been “prepared” for evading birds even before they made their transition to diurnal life. Color itself, although exploited to the full only in the context of diurnality by butterflies, also has a history of adaptive use by moths for startling and warning purposes and for camouflage (witness the defensive flashing of fake “eyes” by hindwing exposure in many saturniids and sphingids, the warning coloration of unpalatable arctiids, and the background-matching colors of cryptic species) (1, 2). The capacity for spectral adornment brought to expression in butterfly aposematism therefore might have been inherited by butterflies from their nocturnal progenitors.

Materials and Methods

Observational Tests. Tests with hand-released lepidopterans were done outdoors, in Florida (Lake Placid, Highlands County) and New York (Ithaca, Tompkins County). Butterflies (identified to species), either caught in the wild or raised from pupae obtained commercially (Greathouse Butterflies) were subjected while being held by hand to hindwing removal. (The hindwing was severed with scissors along a line just distal to the point of articulation of the hindwings with the thorax, so that only a small triangular flap of each hind wing remained; Fig. 1). They then were released in open terrain, and a visual appraisal was made of how their escape flight compared with that of intact individuals of the same species, similarly obtained and released at the site as controls.

The tests with moths (all done in Ithaca) were identical to those with butterflies, except that the moths were captured at an UV light trap to which they had been attracted in the night (two of the moth species differed in that they had been raised in culture). Unlike butterflies, which usually took to the wing promptly when set free, moths often did not take off until they had warmed by shivering. Moths in some cases were identified to genus or family only. Some were available to us as only single specimens, so that we could check their capability to fly without hindwings but not their degree of flight impairment relative to intact controls.

If held captive for any extended time, the butterflies and moths used in these observational tests (like the *P. rapae* and *L. dispar* used in the quantitative tests) were maintained in cages with access to diluted honey solution or Gatorade presented on soaked wicks. They seemed to thrive under these conditions.

Hindwing Area. The ratio of hindwing area to total wing area was determined by tracing the outline of the four wings on translucent paper, cutting out the resulting paper images, and computing the ratio of the weight of the hindwing cutouts to the weight of all four wing cutouts. Ratios were expressed as percentages.

Quantitative Data (*P. rapae* and *L. dispar*). *P. rapae* adults were collected in the field near Ithaca, New York, and tested outdoors. They were released within an open space monitored by a pair of camcorders and in some instances were recaptured for retesting. Tests with *L. dispar* males (sent to us as pupae from cultures maintained by the U.S. Department of Agriculture) were done in a $7.7 \times 6.1 \times 2.1$ m walk-in flight chamber enclosed by mosquito netting. A bucket holding 10 to 15 moths (8 d minimum age), either all de-winged or all intact, was introduced into the center of the enclosure where it was within the field of view of two camcorders that continuously recorded as the males spontaneously took to flight.

Position Tracking. The two camcorders used to obtain 3D trajectories were aligned with perpendicular views of a common space or “tracking volume” in an arrangement similar to that described by Zeil (19). Known methods (19–26) then were used to compute a flight trajectory from each sequence of video images.

Error Estimation. The error in position measurement of *P. rapae* and *L. dispar* in the 3D trajectories derives from three principal sources: the physical alignment of the camcorders, the resolution of the camcorder images, and the determination of the insect’s center of mass within each camcorder image. To estimate the aggregate error, the ends of a 1-m rod were tracked as it was moved through different orientations and locations throughout the tracking volume. The rms error in the computed length of the rod was used to estimate the variances in position (27). The procedure was repeated, yielding in the worst case an rms error in the length dimension of 0.053 m (for a sample of 31 positions of the rod), indicative of position errors of $dx = 0.04$ m, $dy = 0.04$ m, $dz = 0.12$ m. The threefold larger error in the vertical dimension is caused by the 240-line vertical resolution of the de-interlaced video images, compared with the 720-line horizontal resolution. The estimated measurement errors (shown in Fig. 2E) are much smaller than a typical radius of curvature (see Table 2). To check the accuracy of these measurements, we also tracked a dense object in ballistic motion. For seven trajectories we found a free-fall acceleration of 9.76 ± 0.73 m/s² (mean \pm SD), a figure within 0.5% of the true value.

Analysis of Flight Trajectories. The mean magnitudes of speed (v), acceleration (a), and turning acceleration (a_N) pertinent to *P. rapae* and *L. dispar* were computed from the 3D trajectories. Most trajectories were missing points corresponding to times during a flight in which the insect was not visible to one or the other camcorder. Only those trajectories spanning 2 or more seconds for *L. dispar* or 1 or more seconds for the faster *P. rapae* and missing no more than 50% of their points were analyzed. The computation of each kinematic parameter (v , a , a_N) required taking one or more derivatives of a discretely sampled function for each point in a trajectory. For all such derivatives, we used a 5-point least squares parabolic fit as described by Lanczos (28) and as applied to the flight trajectories of bats by Rayner and Aldridge (24).

To determine the mean speed, v , of a trajectory, we computed the instantaneous velocity (\vec{v}), the derivative of position with respect to time, and then averaged the magnitude of this instantaneous velocity over the entire recorded flight. The mean magnitude of the acceleration, a , was found in an analogous way.

To ascertain the component of acceleration strictly attributable to changes in direction, we determined the unit normal vector (\hat{N}), equivalent to a vector of unit length directed from a point on the flight path to the center of the turn undertaken at that point. The unit normal vector was computed from the expression

$$\hat{N}(t) = \frac{\frac{d\vec{T}}{dt}}{\left| \frac{d\vec{T}}{dt} \right|},$$

where

$$\vec{T}(t) = \frac{\vec{v}}{|\vec{v}|}$$

is the unit vector tangent to the curve (29). From the normal vector at each point, we calculated the component of the acceleration parallel to this normal and therefore attributable to an instantaneous change in direction rather than a change in speed. These instantaneous normal accelerations were averaged over a trajectory to yield a_N . We also considered just that component of the normal acceleration lying in the horizontal (x - y) plane (see Results). This

component of the turning acceleration is free from the influence of gravity and is proportional to the net aerodynamic force produced by the flying insect in that direction.

Position data also were used to compute the mean radius of curvature, r . First, an instantaneous radius was computed at each point in a trajectory from the corresponding instantaneous velocity and acceleration values, expressed by

$$\frac{|\vec{v}|^3}{|\vec{v} \times \vec{a}|}$$

(29). These instantaneous values then were averaged over each trajectory to give the mean radius of curvature, r . The instantaneous radius of curvature at a point on a curve is equivalent to the radius of the circle that best approximates the curve at that point (29), and the mean radius of curvature is thus a measure of the typical turning radius in a flight path. For flights with many sharp turns, the mean radius of curvature is low, whereas for nearly linear flights it is large. It provides a global metric for the deviation of a flight path from a straight line.

Wingbeat Frequencies. Wingbeat frequencies were measured using footage from a Phantom V high-speed CMOS video camera. The camera, equipped with a 50-mm lens, was positioned 1.0–1.5 m from a white background, in front of which individual intact and de-winged *P. rapae* and *L. dispar* were released. The insects were filmed at 250 frames per second in free flight, and

their wingbeat period was determined by counting the frames necessary to complete one wingbeat cycle.

Computation of Statistics. Treatments were compared using *t*-tests except for the radius of curvature for which, because of a failure of normality, a Kolmogorov–Smirnov test was used. Sample sizes for the four categories of flight trajectories that were analyzed (*P. rapae* intact and de-winged; *L. dispar* intact and de-winged) are given in Table 2. For both categories of *P. rapae*, the trajectories were not all from separate individuals. The 41 flights entered into the intact and de-winged categories stemmed, respectively, from 17 and 9 individuals.

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